



Two extraordinary new genera and 6 new species of armored scale insects (Hemiptera: Coccoomorpha: Diaspididae: Xanthophthalminae and Ancepaspidinae) from Chile

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We describe 2 new genera and 6 new species of unusual armored scale insects (Hemiptera: Coccoomorpha: Diaspididae) from Chile: ***Austraspis*** Normark, Normark and Amouroux, **gen. n.**; ***Aysenaspis*** Normark, Normark and Amouroux, **gen. n.**; ***Austraspis foye*** Normark, Normark and Amouroux, **sp. n.**; ***Austraspis llanquihue*** Normark, Normark and Amouroux, **sp. n.**; ***Austraspis pehuen*** Normark, Normark and Amouroux, **sp. n.**; ***Austraspis relicta*** Normark, Normark and Amouroux, **sp. n.**; ***Aysenaspis michay*** Normark, Normark and Amouroux, **sp. n.**; and ***Anotaspis paradisi*** Normark, Normark and Amouroux, **sp. n.** *Austraspis* is remarkable for having abdominal segments V and VI free (not fused), with only segments VII and VIII fused to form the pygidium, and in having a proliferation of multilobulate lobes (each with 3 to 6 lobules) on the abdomen. *Aysenaspis* is remarkable for having all 8 abdominal segments free and in having ducts that are 8-shaped at the internal end. Phylogenetic analysis of part of 28S rRNA places the 2 new genera (*Austraspis* and *Aysenaspis*) outside of currently recognized subfamilies of Diaspididae and corroborates the placement of *Anotaspis* in Ancepaspidinae. We place the new genera in the heretofore monotypic taxon **Xanthophthalminae** Ferris, **revived subfamily**. We provide a revised key to the subfamilies of Diaspididae and global keys to all the species of Xanthophthalminae and Ancepaspidinae. The host plants of *Austraspis* are *Araucaria araucana* (Araucariaceae) and *Drimys winteri* (Winteraceae), which both have undergone little morphological change since the Mesozoic. *Austraspis* may also retain a relatively ancient morphology; its pygidial appendages are relatively undifferentiated compared to those of other diaspidids.

Keywords: Gondwana, Neotropical, Patagonia, pupillarial, scale cover

Introduction

The Valdivian temperate rainforests of Chile and Argentina comprise the world's southernmost forests and one of world's most isolated environments—thousands of miles from any other temperate forest, with a cool, moist, oceanic climate year-round. These forests constitute one of the world's 36 biodiversity hotspots, with high endemism of plants and animals; over 70% of their original area has been lost due to human activities as forestry and agriculture (Hora et al. 2022). Their flora seems to be remarkably stable and slow to change: many of the trees, such as *Nothofagus* (Nothofagaceae) and *Drimys*

(Winteraceae) closely resemble their Cretaceous fossil congeners (Poole and Francis 2000, Iglesias et al. 2011).

Seemingly in stark contrast to such ancient, slowly evolving taxa are the armored scale insects (Diaspididae), which originated more recently than most other families of scale insects, yet are nonetheless the most species-rich family due to their rapid diversification (García Morales et al. 2016, Vea and Grimaldi 2016, García Morales 2025). Many armored scale insects are highly invasive economic pests, and in Chile, in particular, an unusually high proportion of the described armored scale insect fauna—nearly 60%—is invasive

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(Miller and Davidson 1990, 2005, Kondo and Watson 2022, Normark et al. 2025). This high proportion may be, at least in part, an artifact of incomplete knowledge of the native fauna. One of us (PA) has been collecting armored scale insects in a wide variety of habitats in Chile since 2015 (Amouroux et al. 2017) and has found a number of undescribed species (Amouroux et al. 2020). The purpose of this article is to describe some of these. Three of the new species are found in temperate rainforests on *Drimys winteri* (Winteraceae); a fourth species is found on *Araucaria araucana* (Araucariaceae), another taxon that, like *Drimys*, has undergone little morphological change since the Cretaceous (Escapa and Catalano 2013). These insects show remarkable features not seen in any previously known subfamily of armored scale insects. We place them in a new genus, *Austraspis* Normark, Normark and Amouroux, **gen. n.**, and argue that, like their hosts, they have retained some relatively ancient morphological characters—specifically, relatively undifferentiated marginal appendages.

In total, we describe 2 new genera and 6 new species, all from native plants. All are morphologically unusual and most fit only uncertainly into existing higher taxa. We tentatively place the 2 new genera and 5 of the 6 new species in the heretofore monotypic taxon **Xanthophthalminae, revived subfamily**. The sixth species we place in the heretofore monotypic genus *Anotaspis* Ferris (subfamily Ancepspidae). We provide a revised key to the subfamilies of Diaspididae and global keys to all the species of Xanthophthalminae and Ancepspidae.

Materials and Methods

Scale insect specimens were removed from the surface of their host plant (leaves or bark) using a minuten pin, without damaging either the plant or the insect's body, and were immediately transferred to 96% or 100% ethanol. In the laboratory, samples were stored at -20°C. Samples collected between 2019 and 2024 were subjected to a nondestructive total genomic DNA extraction protocol, and the cuticle was mounted on a microscope slide as a permanent voucher specimen.

DNA was extracted using the prepGEM Insect DNA extraction kit (ZyGEM, Lane Hamilton, New Zealand) or the PureLink™ Genomic DNA Mini Kit (Thermo Fisher Scientific, USA), following the manufacturer's guidelines, but with 2 modifications: cell lysis was carried out overnight, and final elution was done in 50 µl. We amplified the D2 region of the large ribosomal subunit (28S) with the primers C-28SLong-F (5' GAGAGTTMAASAGTACGTGAAAC 3') and C-28SLong-R (5' TCGGARGGAACCAGCTACTA 3'), as described by Amouroux et al. (2017) using the GoTaq G2 Master Mix (Promega, USA). PCR products were quality-checked via electrophoresis and then sequenced by Genewiz using an ABI 3130XL sequencer. Chromatograms were analyzed with BioEdit.

To the 8 new 28S sequences from new Chilean species were added sequences from 169 other species that were previously reported in Normark et al. (2019), for a total of 177 sequences for phylogenetic analysis. These included all of the sequences for Ancepspidae, Furcaspidae, and the 3 families of outgroups, and a sample of about 10 sequences from each tribe of Aspidiotinae and each subtribe or tribe of Diaspidinae (see Data Availability).

Alignment was performed using MAFFT (Katoh and Standley 2013) and cleaned using BMGE (Criscuolo and Gribaldo 2010). Two different phylogenetic methods were used, following workflows provided by NGPhylogeny.fr (Lemoine et al. 2019): a

Bayesian analysis using MrBayes (Huelsenbeck and Ronquist 2001) and a maximum likelihood analysis using PhyML (Guindon et al. 2010, Lefort et al. 2017). For the Bayesian analysis, 50 million generations were run on 4 chains with a 30% burn-in, print frequency of 25,000, model GTR with Gamma-distributed rates across sites. Posterior probabilities were obtained with PAUP 4 3.99.169.0 ("contree/Majrle" command) from the output of the MrBayes analysis (1,601 trees). For the maximum likelihood analysis, the phylogenetic tree was estimated using PhyML+SMS with the model GTR+G+I. The tree diagram was edited using ITOL (Letunic and Bork 2021).

For light microscopy, DNA vouchers or specimens stored in alcohol were macerated in a 10% potassium hydroxide solution. Then they were washed in distilled water to remove potassium hydroxide and remaining body contents. The cuticles were stained using a mixture of acid fuchsin, distilled water, glycerol, and lactic acid. Then the specimens were dehydrated in acetic acid. Finally, they were transferred to lavender oil until being mounted in Canada balsam on microscope slides.

Mounted specimens were examined using an Olympus BH-2 or Olympus BX41TF phase-contrast microscope (Olympus America, Center Valley, Pennsylvania, USA), and measurements were made with the aid of an eyepiece reticule. Illustrations were made using a Nikon Optiphot compound microscope (Nikon USA, Melville, New York, USA) with a camera lucida. Original drawings of pencil on paper were scanned and then electronically inked and edited using the SketchBook app (Autodesk, Inc., San Rafael, California, USA) on an Apple iPad Pro.

Morphological terminology follows Normark et al. (2019) and Miller and Davidson (2005). The abbreviations L1, L2, and L3 refer to the median, second, and third lobes, respectively. Numbers (counts) refer to one side of the body, unless stated otherwise. Specimen repositories are abbreviated as follows. MEUC, Museo Entomológico de la Universidad de Chile (Museo Luis Peña), Facultad de Ciencias Agronómicas, Universidad de Chile, Santiago de Chile, Chile; MNHN, Museo Nacional de Historia Natural, Quinta Normal, Santiago de Chile, Chile; NHM, Natural History Museum, South Kensington, London, UK; SAGC, Colección Entomológica, Departamento de Laboratorios y Estaciones Cuarentenarias Agrícola y Pecuaria, Servicio Agrícola y Ganadero de Chile, Central, Lo Aguirre, Región Metropolitana de Santiago, Chile; SAGV, Colección Entomológica, Laboratorio Entomológico y Acarología, Servicio Agrícola y Ganadero Valparaíso, Valparaíso, Chile; UMEC, University of Massachusetts Entomology Collection, Amherst, Massachusetts, USA; USNM, United States National Museum, scale insect collection, now (since August 2025) housed at the National Museum of Natural History, Washington, DC, USA.

Nomenclature

This paper and the nomenclatural acts it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is:

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- urn:lsid:zoobank.org:act:EF0D0EB7-84F4-4458-80BC-B353839CC0DF for *Aysenaspis* Normark, Normark & Amouroux

- urn:lsid:zoobank.org:act:CE451F43-C4AE-4EAD-9F5F-7CFCF10676A4 for *Anotaspis paradisi* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:6108AFC3-A1B5-4282-8F59-262B23958BB0 for *Austraspis foye* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:7852EF60-D2E6-49B3-B369-1DC5640163D4 for *Aysenaspis michay* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:874D2EA8-010E-4BDD-AD3D-5B239D7337DF for *Austraspis relicta* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:648C367C-FB35-406F-9197-AC7EFFF0F9C8 for *Austraspis pehuen* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:FB890561-1AD8-4F56-BC1C-380CCBF089DD for *Austraspis llanquihue* Normark, Normark & Amouroux

Results

Results of the Bayesian phylogenetic analysis are shown in Fig. 1. There is strong support (100% posterior probability) for the inclusion of *Anotaspis paradisi*, sp. n., in Ancepaspidinae. There is also strong support (100% posterior probability) for the monophyly of a group comprising the other 3 new species included in the analysis: *Austraspis pehuen*, sp. n.; *Austraspis llanquihue*, sp. n.; and *Aysenaspis michay*, sp. n. But that group falls outside of all the previously recognized subfamilies of Diaspididae. In Fig. 1, it appears as sister to Ancepaspidinae + Aspidiotinae (Fig. 1, Supplementary Fig. S1), but support for that relationship is low (58% posterior probability), and this clade's relationship to the previously recognized subfamilies remains unresolved.

The maximum likelihood analysis failed to recover a monophyletic Diaspididae, instead showing 2 outgroup sequences, the eriococcids *Cryptococcus fagisuga* Lindinger and *Pseudochermes fraxini* (Kaltenbach), nested within the subfamily Ancepaspidinae. But otherwise the subfamilies of Diaspididae are monophyletic and the topology is broadly similar to that seen in the Bayesian results: *Anotaspis paradisi* is nested within Ancepaspidinae with high support, and *Austraspis* + *Aysenaspis* falls outside of the recognized subfamilies, appearing as sister to Aspidiotinae with low support (82% bootstrap) (Supplementary Fig. S2).

Systematics

Xanthophthalminae Ferris, Revived Subfamily

Previously cited as Xanthophthalmini (Ferris 1937, 1938), Xanthophthalminae (Borchsenius 1965, 1966, Williams 1969).

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Description. Found on leaves and bark of host; scale cover consisting mainly or entirely of exuviae, with at most only a narrow fringe of additional wax. On microscope slide, adult female without gland spines and without regularly arranged plates, though a few unsclerotized lobules may appear plate-like; dorsal ducts minute, 8-shaped or 2-barred; abdominal segments V and VI free; segments VII and VIII free or fused to

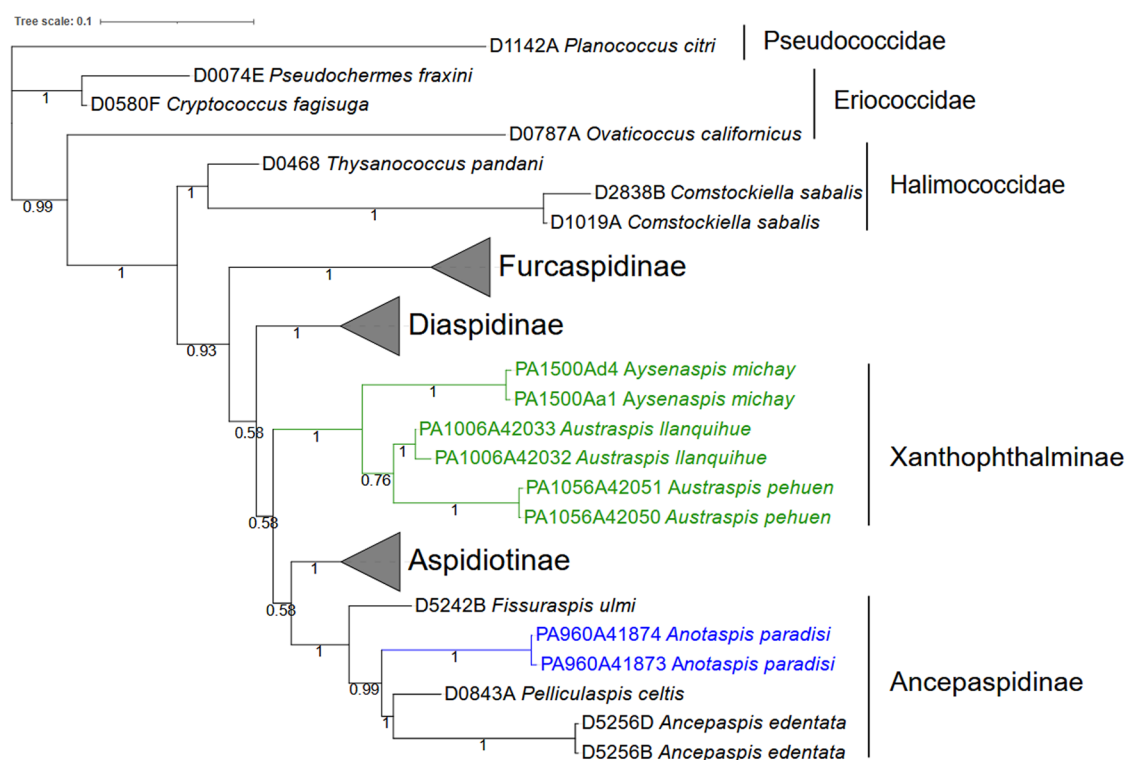


Fig. 1. Phylogenetic tree of Diaspididae inferred from a Bayesian analysis of a fragment of the large ribosomal subunit (28S). Numbers beneath internodes are posterior probabilities.

form pygidium; antenna with 1 to 4 setae; perispiracular pores, when present, quinquelocular; perivulvar pores absent; lobes (trullae), when present, often multilobulate or bilobulate; cephalothorax with or without a submarginal row of gland tubercles.

Distribution. Mexico and Cuba to Chile.

Included genera. *Austraspis* Normark, Normark and Amou-
roux (**gen. n.**); *Aysenaspis* Normark, Normark and Amou-
roux (**gen. n.**); *Xanthophthalma* Cockerell and Parrott in Cockerell,
1899.

Remarks. *Xanthophthalma* was placed in its own tribe by Ferris (1938) and its own subfamily by Borchsenius (1966). Ferris placed Xanthophthalmini in the subfamily Diaspidinae, where he also placed several of the genera now in Ancepspidini (Ferris 1941, SIII-309). Takagi (2002) remarked enigmatically that “not all of the known forms of diaspidids readily find their places” in his classification; he opined that *Xanthophthalma* “should be kept in the Diaspididae, because the adult female is armoured with the nymphal exuvial casts” but he did not assign it to any subfamily or tribe. Normark et al. (2019), who based their classification on Takagi’s (2002), moved *Xanthophthalma* to Halimococcidae without comment; here we are treating Xanthophthalminae as a subfamily of Diaspididae.

Aysenaspis is similar to *Xanthophthalma* in several respects: all 8 abdominal segments free, complete absence of any marginal or submarginal appendages (lobes, gland spines, plates, gland tubercles) in both the adult and the second instar, and—most strikingly—minute ducts that are 8-shaped at the internal end, unlike the ducts of any other diaspidid. But in other characters *Aysenaspis* differs from *Xanthophthalma* and instead resembles *Austraspis*: antenna with 4 setae (1 seta in *Xanthophthalma*) and presence of quinquelocular pores near both spiracles (absent in *Xanthophthalma*). *Austraspis* may seem strikingly different from the other 2 genera in having a proliferation of lobes and lobules on the abdomen, while the others lack them entirely, but abdominal lobes have been lost many times in Diaspididae, and higher taxa based on this character have often turned out to be spurious; cf Protodiaspidina, Rugaspidiotini, Thysanaspini, Ulucoccinae (Takagi et al. 1997, Normark et al. 2019). The 3 genera placed here all have abdominal segments V and VI free, not incorporated into a pygidium; they all lack plates and gland spines and have minute ducts.

Another striking similarity uniting the species of Xanthophthalminae is the form of the scale cover. Unlike most diaspidids, none of the species of Xanthophthalminae has an extensive secreted scale cover extending beyond the borders of the second-instar exuviae. Nor is any pupillarial, remaining enclosed within a capsule formed by the exuviae of the second instar. Instead, all species of Xanthophthalminae apparently have a second instar with a dehiscent cuticle, splitting into a flat ventral portion that adheres to the plant surface and a dorsal portion that comprises the entire dorsal scale cover of the adult, with any secreted wax occurring only in the narrow gap between the 2 portions of the second-instar cuticle. For *Xanthophthalma*, “a very small amount of wax secretion may occur about the exuviae, although at times it appears to be lacking” (Ferris 1938, S2-174). The same could be written about all the species of *Austraspis* and *Aysenaspis*. The main difference between the scale covers of *Austraspis* and

Aysenaspis, on the one hand, and *Xanthophthalma*, on the other, is that the second-instar exuviae of *Austraspis* and *Aysenaspis* are coated with white wax, while those of *Xanthophthalma* consist of exposed sclerotized cuticle, without wax.

Unfortunately, no DNA is yet available for *Xanthophthalma*, and the hypothesis of its relationship to *Aysenaspis* and *Austraspis* remains somewhat conjectural, but pending further evidence we have preferred to accommodate the unusual new genera within existing or previously proposed higher taxa rather than erect new taxa.

Austraspis Normark, Normark, and Amou-
roux, **Gen. n. Type species.**

Austraspis foye Normark, Normark, and Amou-
roux, sp. n.

Description. Occurring on the leaves or bark of the host; adult female partially enclosed within second-instar exuviae; first exuviae retained at anterior margin of second exuviae. Slide-mounted adult female without gland spines; without regularly arranged plates (though a few unsclerotized lobules may appear plate-like); with all 8 abdominal segments free, or with abdominal segments VII and VIII apparently fused; dorsal ducts 2-barred, minute; antenna with multiple setae; quinquelocular pores present near anterior and posterior spiracles; sclerotized lobes (trullae) always bilobulate or multilobulate, never unilobulate; lobe present on each of abdominal segments VI–VIII, present or absent on each of segments II–V; ventral submargin of cephalothorax with row of gland tubercles.

Distribution. Chile, from Coquimbo (30.3°S) to Tierra del Fuego (53.7°S).

Included species. *Austraspis foye*, **sp. n.**; *Austraspis llanquihue*, **sp. n.**; *Austraspis pehuen*, **sp. n.**; *Austraspis relict*, **sp. n.**

Etymology. The name is taken from the Latin adjective *australis*, southern, and the Greek feminine noun *aspis*, shield. It reflects 2 facts about the type localities of the included species: all of them are in Chile, the southernmost country in the world, and one of them is at 53.7° S latitude, one of the southernmost localities from which scale insects have ever been collected.

Remarks. The proliferation of multilobulate lobes seen in *Austraspis* is unique and should permit separation from all other genera. But to date, *Austraspis* species have been misidentified in collections. Like another extraordinary taxon from the Americas, *Thysanaspis denmorum* Normark and Okusu, specimens of *Austraspis* have languished in collections under the name *Protodiaspis* sp. *Austraspis* indeed resembles *Protodiaspis* in having minute 2-barred ducts present and plates absent, and also resembles some *Protodiaspis* species in having abdominal segments V and VI free, pores by the anterior spiracles present, a row of duct tubercles present on the ventral submargin of the cephalothorax, and gland spines absent. Some *Austraspis* species resemble some *Protodiaspis* species in having the lobules of L2 well separated, or in having lobules serrate along the apical margin. But *Austraspis* consistently differs from *Protodiaspis* in having multisetose antennae (antennae unisetose in *Protodiaspis*) and in having bilobulate or multilobulate L1 (L1 at most unilobulate in *Protodiaspis*) and multilobulate L2 and L3 (at most bilobulate in *Protodiaspis*).

Early in the present investigation, one of us (BBN) misidentified an *Austraspis* specimen as *Lopholeucaspis* sp. *Austraspis* indeed resembles *Lopholeucaspis* in having multisetose antennae, a row of duct tubercles on the ventral submargin of the cephalothorax, 5-locular pores near the anterior spiracles, and small 2-barred ducts. But *Austraspis* differs from *Lopholeucaspis* in having multilobulate lobes (all lobes unilobulate in *Lopholeucaspis*) and pores by the posterior spiracle (absent in *Lopholeucaspis*), in lacking plates and perivulvar pores (both present in *Lopholeucaspis*), and in being only partially enclosed within the exuviae of the second instar (*Lopholeucaspis* fully enclosed within a puparium).

***Austraspis foye* Normark, Normark, and Amouroux, sp. n.**

Holotype. Adult female, ex *Drimys winteri* J. R. Forst. & G. Forst., CHILE, Magallanes, Punta Arenas, Sendero Monte Tarn, -53.8, -71.0, 22.i.2020, M. Sepúlveda, 10788/20 (MNHN)

Paratypes. Seven adult females, same slide as holotype (MNHN); 11 adult females, 2 second-instar female exuviae, same data as holotype (SAGC); 2 adult females, 1 second-instar female exuviae, CHILE, Aysén, Puerto Aysén, 13.xii.2005, SAG 69977/05 (SAGC); 29 adult females, 1 second-instar female, 11 second-instar female exuviae, and 8 crawlers, ex *Drimys winteri*, CHILE, Magallanes, Punta Arenas, Predio San Juan, -53.7221, -70.9683, 28.x.2020, M. Sepúlveda, PA1110A, all to MNHN (9 slides, PA1110A-01, PA1110A-02, PA1110A-03, PA1110A-06, PA1110A-08, PA1110A-09, PA1110A-10, PA1110A-11, PA1110A-12) except 1 slide each to USNM (3 adult females, 1 second-instar exuviae, PA1110A-04), NHM

(2 adult females, 2 second-instar exuviae, PA1110A-07), and UMEC (3 adult females, 1 second-instar exuviae, PA1110A-05).

Adult female. In life (Fig. 2), on underside of leaf, tucked into revolute leaf margin near base of leaf, or along midrib; elongate dorsal scale cover, consisting of exuviae of second instar, white; exuviae of first instar marginal, orange; exuviae of second instar orange but usually covered with white wax, partially enclosing body of adult female; body of live female pink to purple. On microscope slide (Fig. 3), 850 to 1150 (median 950, $n=17$) μm long, 320 to 600 (median 470) μm wide, broadest at mesothorax or metathorax. Body outline oval, elongate oval, or obovate; cuticle remaining membranous. Abdominal segments I–VI free; segments VII and VIII fused. Antenna simple, with 4 setae. Distance between antennae 57 to 108 (median 78) μm . Eye a pigmented tubercle on submargin of venter laterad of antenna. Anterior spiracle with 5 to 17 (median 9) quinquelocular disc pores; posterior spiracle with 3 to 11 (median 6) pores. Derm of submedial areas of venter beset with minute spicules from prothorax to abdominal segment V or VI. **Lobes.** Abdominal segments VI–VIII and usually also segment V each with a multilobulate lobe (trulla) projecting from body margin; lobules of each lobe closely appressed, sometimes partially fused; lobes separated by a space about as wide as one lobule. Each lobule subcylindrical, mostly membranous, with hyaline serrate crest at apex. L1 with 2 to 4 (median 3) lobules, L2 and L3 each with 3 to 6 (median 4) lobules; abdominal segment V (L4) with 0 to 5 lobules; abdominal segments II–IV usually without lobules, rarely with up to 3 lobules each, these often membranous. **Plates** absent, though a few lobules (usually



Fig. 2. Habitus of *Austraspis foye* sp. n. A) Adult females on the border of the revolute leaf margin, near base of leaf. B) longitudinal cut of the revolute margin, exposing purple bodies of live adult females. Leaf of *Drimys winteri*, Sendero Monte Tarn, Magallanes.

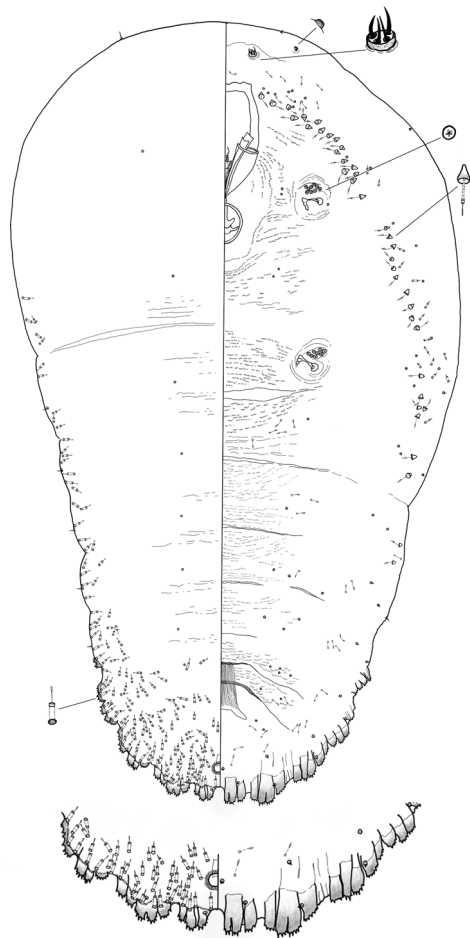


Fig. 3. *Austraspis foye* sp. n., slide-mounted adult female. The dorsal surface is illustrated on the left side of the figure and the ventral surface on the right.

anteriormost 1 or 2 lobules of lobe) sometimes membranous and plate-like. **Gland spines** absent. **Gland tubercles.** Submargin of cephalothorax with a dense, continuous row of gland tubercles, with a total of 41 to 53 (median 45) gland tubercles on each side of body. **Ducts.** Dorsal ducts 2-barred, very small (2 to 3 μm wide, 6 to 8 μm long); abundant in a broad submarginal band on abdominal segments V–VIII, also present in a narrower band along body margin of segments I–IV, and in submedial areas of segments VI–VIII. Ventral microducts present in a narrow band around submargin of cephalothorax, laterad of duct tubercles; a few also present in submedial rows on abdominal segments II–V, and scattered elsewhere on body. **Cicatrices** absent. **Paraphyses** absent. **Anal opening** subcircular, 10 to 17 (median 12) μm long, 11 to 19 (median 12) μm wide, located on posterior submargin; distance from margin 22 to 50 (median 35) μm or 2 to 5 (median 3) anal diameters. **Perivulvar pores** absent.

Second-instar female. On microscope slide (Fig. 4), 910 (n=1) μm long, 360 μm wide, broadest at mesothorax. Body outline elongate oval; cuticle becoming sclerotized throughout. Segments VII–VIII fused to form pygidium. Antenna simple, with 4 setae. Distance between antennae 35 μm . Eye a pigmented tubercle on submargin of venter anterolaterad of antenna. Anterior spiracle with 3 quinquelocular disc pores; posterior

spiracle with 1 pore. **Lobes.** Every abdominal segment with a multilobulate lobe (trulla) projecting from body margin; lobules of each lobe slightly separated from each other, sclerotized or hyaline, forming one or more acute points (triangular or strongly serrate); one (usually triangular) lobule in each lobe subtended by a pair of paraphysis-like basal scleroses longer than lobule; L1 and L2 each with 3 lobules, L3 with 3 to 4, L4 with 2 to 4, abdominal segment IV with 3, III with 3, II with 2, I with 3; row of lobules on abdomen contiguous with row of gland tubercles on cephalothorax, with structures on abdominal segment I and metathorax intermediate between typical lobules and typical gland tubercles. Plates absent. Gland spines absent. Gland tubercles: submargin of cephalothorax with a row of gland tubercles, with a total of 17 to 26 gland tubercles in each side of body. Ducts: dorsal ducts 2-barred, very small (2 to 3 μm wide, 6 to 10 μm long); sparsely distributed across abdominal segments V–VIII, and submarginally on segments I–IV. Ventral microducts numerous submarginally on cephalothorax. Cicatrices absent. Anal opening subcircular, 8 μm in diameter, located on posterior submargin; distance from margin 40 μm or 5 anal diameters.

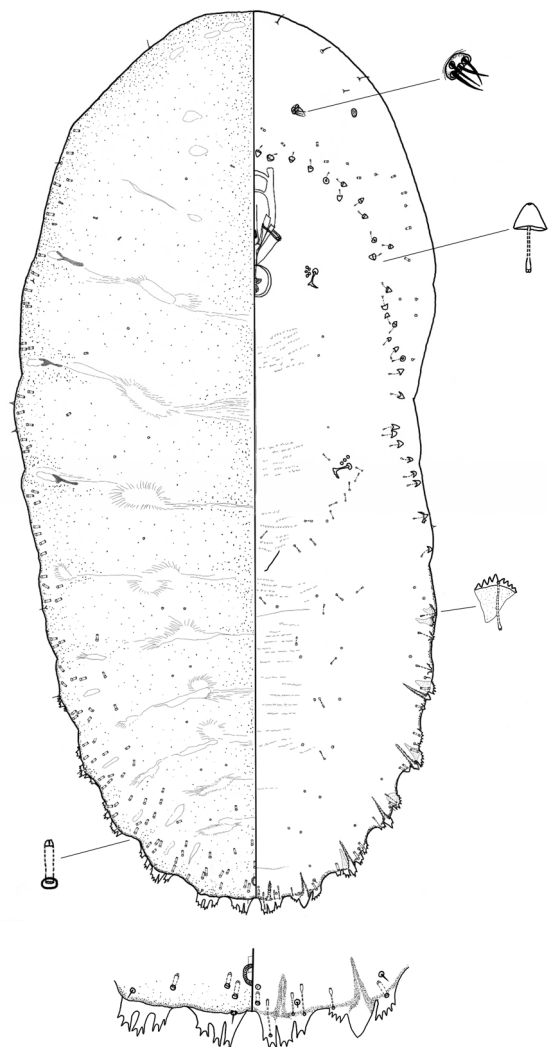


Fig. 4. *Austraspis foye* sp. n., slide-mounted second-instar female.

DNA sequence of a fragment of cytochrome oxidase I from the type series of *Austraspis foye* has been deposited in GenBank, accession number PQ219562.

Etymology. The specific epithet is a Mapuche name for the host. It is an uninflected noun in apposition.

Remarks. *Austraspis foye* is extremely similar to the other 2 species of *Austraspis* that feed on *Drimys winteri*. Based on morphology alone we likely would have lumped them together, but samples of *A. foye* and *A. llanquihue* are more than 12% divergent at the barcoding region of COI, indicating that they are almost certainly separate species. We do not have molecular data from *A. relictata*, but it is from a geographically distant, anciently separated relict forest patch (Cádiz et al. 2019), and for the few characters that separate *A. foye* and *A. llanquihue*, *A. relictata* differs from both. The 3 species differ quantitatively in the expression of the secretory system, with *A. relictata* having the greatest number of pores, gland tubercles, and lobules, *A. llanquihue* having the fewest, and *A. foye* having an intermediate number. No single character separates the species, but the combination the following 3 characters should be sufficient to do so. *A. foye* has: 3 to 11 (median 6) pores by the posterior spiracle (2 to 5, median 4, in *A. llanquihue*, 11 to 13 in *A. relictata*); 5 to 17 (median 9) pores near the anterior spiracle (4 to 6, median 5, in *A. llanquihue*, 13 to 15 in *A. relictata*); 41 to 53 (median 45) gland tubercles on each side of the body (31 to 45, median 41, in *A. llanquihue*, 71 to 92 in *A. relictata*).

***Austraspis llanquihue* Normark, Normark, and Amouroux, sp. n.**

Holotype. Adult female, ex *Drimys winteri*, CHILE, Los Lagos, Puerto Montt, -41.5161, -72.6041, 22.ii.2019, P. Amouroux, PA1006A-06 (MNHN).

Paratypes. Two adult females, same data as holotype, PA1006A-01 (MNHN); one adult female, same data as holotype, PA1006A-05 (USNM); one adult female, same data as holotype, PA1006A-02 (NHM); one adult female, same data as holotype, PA1006A-03 (UMEC); one adult male, same data as holotype, PA1006A-07 (MNHN); one adult male and one second-instar female exuviae, same data as holotype PA1006A-04 (USNM).

Adult female. In life (Fig. 5), on the bark; appearing mainly white, due to coating of white wax on elongate second-instar exuviae; first-instar exuviae marginal, yellow-orange to orange-brown. On microscope slide (Fig. 6), 900 to 1050 μ m long, 370 to 430 μ m wide, broadest at metathorax. Body outline elongate oval; cuticle membranous to slightly sclerotized. Segments VII and VIII free or fused. Antenna simple, with 4 setae. Distance between antennae 64 to 67 μ m. Eye a sclerotized disc on submargin of venter laterad of antenna, often inconspicuous. Anterior spiracle with 4 to 6 (median 5) quinquelocular disc pores; posterior spiracle with 2 to 5 (median 4) pores. Derm of submedial areas of venter beset with minute spicules from prothorax to abdominal segment V or VI. **Lobes.** With 2 to 6 pairs of multilobulate lobes projecting from body margin; each lobe with 2 to 6 lobules. Each lobule membranous at base and hyaline or sclerotized at apex, with serrate apical margin; with 11 to 20 (median 13) lobules on each side of body. **Plates** absent.



Fig. 5. Habitus of *Austraspis llanquihue* sp. n. Arrows indicate scale covers of adult females, immature females, and immature males on bark of the trunk of *Drimys winteri* from Puerto Montt, Los Lagos.

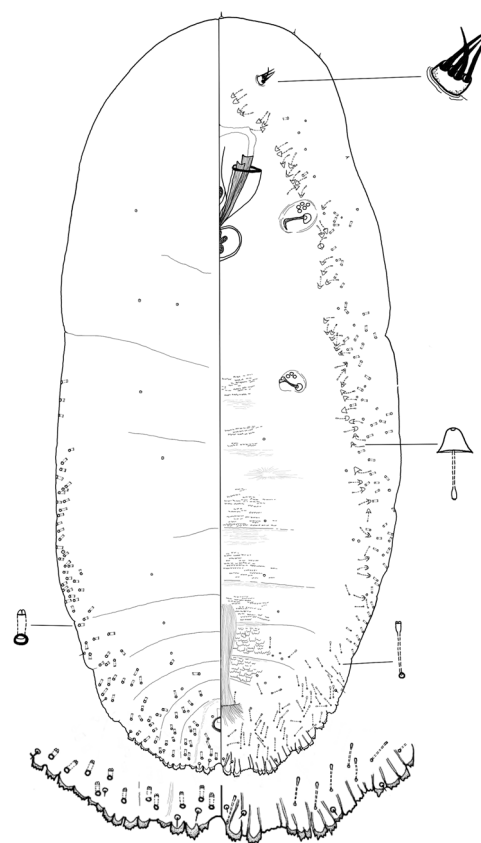


Fig. 6. *Austraspis llanquihue* sp. n., slide-mounted adult female.

Gland spines absent. **Gland tubercles.** Submargin of cephalothorax and abdominal segments I and II with a continuous row of gland tubercles, with a total of 31 to 45 (median 41) gland tubercles on each side of body. **Ducts.** Dorsal ducts 2-barred, very small (2 to 3 μ m wide, 6 to 9 μ m long), abundant in a broad submarginal band on abdominal segments V–VIII, also present in a narrower band along body margin of segments I–IV, and in submedial areas of segments IV–VIII. Ventral microducts present in a submarginal band around entire body, though absent or very sparse on head; long, narrow, and abundant in a wide band on abdominal segments VIII–VI, becoming shorter, broader, and sparser, in a narrower band, anteriorly; a few present in submedial areas of segments VIII–V. **Cicatrices**

absent. **Paraphyses** absent. **Anal opening** subcircular, 11 to 15 (median 14) μm in diameter, located on posterior submargin, 22 to 30 (median 25) μm or 1.7 to 2 (median 1.8) anal diameters from margin. **Perivulvar pores** absent.

Adult male. Apterous.

DNA sequence of fragments of large ribosomal subunit (28S) and cytochrome oxidase I of members of the type series of *Austraspis llanquihue* have been deposited in GenBank: accession numbers PQ219560 (COI) and PQ211156–PQ211157 (28S).

Etymology. The specific epithet refers to the province that includes the type locality. It is an uninflected noun in apposition.

Remarks. For a discussion of how to separate this from the other, morphologically very similar species that feed on *Drimys*, see the remarks under *A. foye*.

***Austraspis pehuen* Normark, Normark, and Amouroux, sp. n.**

Holotype. Adult female, ex leaf of *Araucaria araucana* (Molina) K. Koch, CHILE, Araucanía, Malleco, Parque Nacional Nahuelbuta, -37.80432, -73.01624, 7.x.2019, P. Amouroux, PA1056A-0290 (MNHN)

Paratypes. All from leaves of *Araucaria araucana*, Parque Nacional Nahuelbuta: 2 adult females, same slide as holotype (MNHN); 1 adult female, 7–8.xii.1992, T. Curkovic (MEUC); 4 adult females, 4 second-instar female exuviae, 8.xii.1992, T. Curkovic (2 slides, MEUC); 1 adult female, 8.xii.1992, T. Curkovic (USNM); 1 adult female, 7.xii.1992, T. Curkovic (MEUC); 4 adult females, 19.i.1993, G. Barría (MEUC); 3 adult females, 21.i.1993, G. Barría (MEUC).

Adult female. In life, on the upper surface of leaves; elongate, highly convex, appearing all white; scale cover mainly consisting of exuviae of second-instar female, with patina of white wax and also usually coated with white commensal fungus; exuviae of first instar at anterior margin; body of live female purple (Fig. 7). On microscope slide (Fig. 8), 680 to 780 (median 750) μm long, 500 to 610 (median 580) μm wide, broadest at metathorax. Body outline broadly oval. Segments VII–VIII fused. Cephalothorax strongly sclerotized at full maturity. Antenna simple, with 4 setae. Distance between antennae 80 to 105 (median 90) μm . Eye a slight tubercle on ventral submargin laterad of antenna. Anterior spiracle with 1 to 5 (median 3) trilobular disc pores; posterior spiracle with 1 to 3 (median 1) pores. **Lobes.** Abdominal segments II–VIII each with a bilobulate or multilobulate sclerotized or hyaline lobe (trulla) projecting from margin. Lobules of each lobe separate (not conjoined), each with a broad basal sclerosis acute at anterior end, or pair of paraphysis-like basal scleroses convergent at anterior end, scleroses each 2 to 4 times length of lobule. Lobules variable in shape from simple and rounded, to slightly notched, to deeply serrate, generally becoming broader, more deeply serrate, and less sclerotized (more hyaline to membranous) anteriorly. Lobules almost uniformly spaced on segments VI–VIII, making assignment of lobules to specific lobes or segments slightly conjectural: L1 with 2 to 3 lobules (usually 3),



Fig. 7. Habitus of *Austraspis pehuen* sp. n. Adult and immature females on upperside of an infested leaf of *Araucaria araucana*, Parque Nacional Nahuelbuta, Araucanía. Note fungal mycelium coating the scale covers, and spherical fungal fruiting bodies.

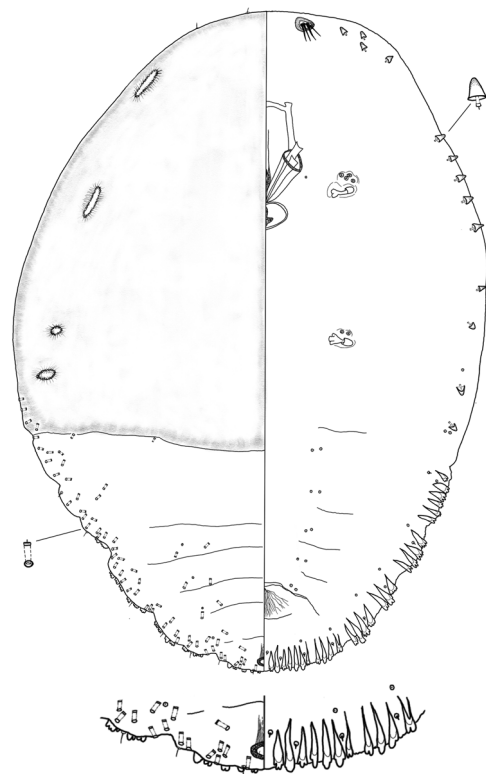


Fig. 8. *Austraspis pehuen* sp. n., slide-mounted adult female.

L2 with 4 to 6 (usually 4), L3 with 3 to 5 (median 4), segment V with 2 to 5 (median 4); IV with 3 to 5 (median 4); III with 0 to 5 (median 4), II with 0 to 6 (median 3); segment I without lobules, rarely with a single membranous lobule; with a total of 17 to 29 lobules on each side of body. **Plates** absent, but some lightly sclerotized lobules on anterior segments becoming plate-like. **Gland spines** absent. **Gland tubercles.** Ventral submargin of cephalothorax with a sparse row of 8 to 14 (usually

11) gland tubercles, extending from head to metathorax. **Ducts.** Dorsal ducts 2-barred, very small (2 to 4 μm wide, 7 to 9 μm long); present in a diffuse band along submargin of abdomen and metathorax; a few also present submedially (2 to 4 on each of segments II–IV). Dorsal ducts absent from mesothorax, prothorax, and head. Ventral microducts absent. **Cicatrices** absent. **Anal opening** subcircular or rarely subtriangular, usually appearing slightly wider than long (apparently due to being usually set at an angle, with posterior edge further ventrad than anterior edge), 10 to 13 (median 11) μm long, 12 to 18 (median 14) μm wide, located on posterior submargin, 15 to 35 (median 29) μm 2.0 to 3.3 (median 2.9) anal lengths from margin. **Perivulvar pores** absent.

DNA sequences of a fragment of the large ribosomal subunit (28S) and cytochrome oxidase I of members of the type series of *Austraspis pehuen* have been deposited in GenBank, accession numbers PQ219561 (COI), PQ211153 (28S).

Etymology. The specific epithet is the Mapuche name of the host. It is an uninflected noun in apposition.

Remarks. *Austraspis pehuen*, the only species of *Austraspis* known to feed on *Araucaria*, is strikingly different from its congeners, which all feed on *Drimys*, and could potentially be regarded as a separate genus. The lobules of *Austraspis pehuen* are separate, sclerotized, and subtended by paraphysis-like basal scleroses, whereas those of the other species are appressed together and basally membranous with a hyaline crest, without scleroses. *A. pehuen*'s lobules are variable in shape, ranging from simple and entire on segment VIII to extensively notched along the apical margin on anterior segments, but generally with rounded apices; those of the other species are all serrate, with a series of acute apices. *A. pehuen* also differs from the other species in having a more compact body, only slightly longer than wide (about twice as long as wide in the other species); cephalothorax sclerotized at full maturity (membranous in the other species); and only a sparse row of duct tubercles, 8 to 14 total on each side (dense row, 31 to 81 on each side, in the other species).

***Austraspis relictata* Normark, Normark, and Amouroux, sp. n.**

Holotype. Adult female, ex *Drimys winteri*, Parque Nacional Fray Jorge, -30.66252, -71.68269, 26.x.2022, coll. Enzo Solis (MNHN).

Adult female. In life (Fig. 9), on underside of leaf, tucked into revolute leaf margin near base of leaf, or along midrib; scale cover elongate, white, with tan exuviae of first instar at anterior end; scale cover consisting of 3 nested layers of similar size: visible white scale cover of second instar, exuviae of second instar, thin white scale cover of adult female; body of live female white, becoming lavender. On microscope slide (Fig. 10, n = 2), 1.1 mm long, 0.5 to 0.6 mm wide, broadest at mesothorax or metathorax. Body outline oval; cuticle remaining membranous. Abdominal segments VII–VIII fused. Antenna simple, with 4 setae. Distance between antennae 75 to 93 μm . Eye a pigmented tubercle on submargin of venter laterad of antenna. Anterior spiracle with 13 to 16 quinquelocular disc pores; posterior spiracle with 9 to 13 pores. Derm of submedial areas of venter beset with minute spicules from prothorax to abdominal segment V or VI. **Lobes.** Abdominal segments V–VIII each with a multi-lobulate lobe (trulla) projecting from body margin; lobules of

each lobe closely appressed, sometimes partially fused; lobes separated by a space about as wide as one lobule. Each lobule subcylindrical, mostly membranous, with serrate hyaline crest along apical margin, often with one microduct opening on ventral surface near apex of membranous portion. L1 with 3 lobules, L2–L3 each with 4 to 5 lobules; L4 with 3 to 6 lobules; abdominal segment IV with 2 to 4 tubercles on margin, these variable, mostly simple and membranous but sometimes with serrated, hyaline apical margin like a lobule, or with a slightly fimbriate, membranous apical margin; abdominal segment III with 3 to 5 membranous tubercles on margin, these variable, some conical and supplied with a duct like a gland tubercle, others more rectangular, sometimes very slightly fimbriate, with or without duct. **Plates** absent. **Gland spines** absent. **Gland tubercles.** Submargin of cephalothorax and abdominal segments I and II with a dense, continuous row of gland tubercles, with a total of 71 to 92 gland tubercles on each side of body. **Ducts.** Dorsal ducts 2-barred, very small (3 to 4 μm wide, 7 to 12 μm

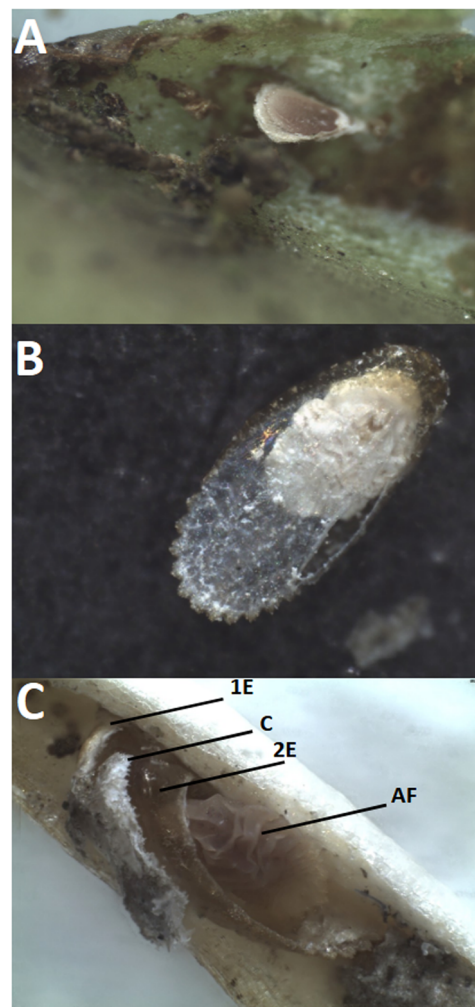


Fig. 9. Habitus of *Austraspis relictata* sp. n. A) Ventral view of fresh second instar female. B) Ventral view of adult female within cuticle of second instar; note partial rupture along seam between dorsal and ventral portions of second-instar cuticle; photographed after being preserved in ethanol. C) Adult female (AF) partially enclosed within dorsal portion of second-instar exuviae (2E), beneath dislodged whitish wax coating of second-instar exuviae (C) and first-instar exuviae (1E); photographed after being preserved in ethanol; on leaf of *Drimys winteri*, Parque Nacional Fray Jorge, Coquimbo.

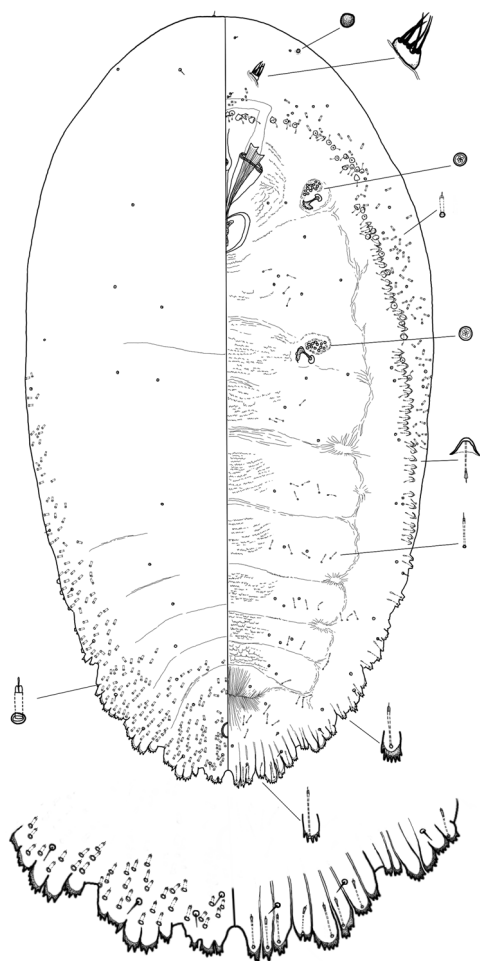


Fig. 10. *Austraspis relictus* sp. n., slide-mounted adult female.

long); abundant in a broad submarginal band on abdominal segments V–VIII, also present in a narrower band along body margin of segments I–IV, and in submedial areas of segments VI–VIII. Ventral microducts present in a narrow band around entire cephalothorax, laterad of duct tubercles; a few also present in submedial rows on abdominal segments II–V, and scattered elsewhere on body. Cicatrices absent. Paraphyses absent. Anal opening subcircular, 10 to 18 (median 12) μm in diameter, located on posterior submargin, 22 to 30 (median 25) μm , about 2 anal diameters, from margin. Perivulvar pores absent.

Etymology. The specific epithet is the feminine form of Latin *relictus*, past participle of *relinquo*, abandon, relinquish. It refers to the habitat of the type locality, the northernmost relict patch of Valdivian rainforest (Cádiz et al. 2019).

Remarks. *A. relictus* is very similar to the other 2 species that feed on *Drimys*; for a discussion of how to distinguish them, see the remarks under *A. foye*.

Aysenaspis Normark, Normark, and Amouroux, Gen. n

Type species. *Aysenaspis michay* Normark, Normark, and Amouroux, sp. n. Scale cover consisting mainly of exuviae of second instar. Slide-mounted adult female without gland spines, gland tubercles, plates, or sclerotized lobes; with 8 free

abdominal segments, none fused; dorsal ducts 8-shaped at internal end, minute; antenna with 4 setae; quinquelocular pores present near anterior spiracles.

Etymology. The name refers to the region (Aysén) in which the type series was collected.

Remarks. *Aysenaspis* is most similar to *Xanthophthalma*, which it resembles in having: minute, short ducts that are 8-shaped at the internal end, on both dorsum and venter; all 8 abdominal segments free, with indentations in the body margin between segments V–VIII; scale cover consisting almost entirely of exuviae, with just a thin crust of wax along the margin; and complete absence of lobes, gland spines, gland tubercles, and plates. *Aysenaspis* differs from *Xanthophthalma* in having: pores by the anterior and posterior spiracles (pores absent in *Xanthophthalma*) and multisetose antennae (antennae unisetose in *Xanthophthalma*).

Aysenaspis michay Normark, Normark, and Amouroux, sp. n.

Holotype. Adult female, ex *Berberis trigona* Kunze ex Poepp. & Endl., CHILE, Aysén, Coyhaique, Punta Arenas, Lago Frío, -45.69221, -71.96206, 22.i.2020, A. Catrilef, SAG Folio Prot. 9279/19 (MNHN)

Paratypes. Three adult females, same slide as holotype (MNHN); 3 adult females, 1 second-instar female exuviae, same data as holotype (SAGC).

Adult female. In life, scales on bark of mature twigs of *Berberis trigona*, oval, appearing white, mainly due to white patina of wax on exuviae of second instar exuviae; some individuals under plant epithelium, thus taking on bark color; body of live female purple. On microscope slide (Fig. 11), 830 to 850 μm long, 490 to 500 μm wide at full maturity, with sclerotized cephalothorax ($n=2$), teneral females smaller (450 to 590 μm long, 270 to 330 μm wide, $n=5$), broadest at mesothorax. Body outline obovate; cuticle of cephalothorax and posterior end of abdomen (segments VIII, VII, and part of VI) sclerotized at full maturity. All abdominal segments (I–VIII) free; none fused. Antenna simple, with 4 setae. Distance between antennae 70 to 78 μm at full maturity, 45 to 73 μm when teneral. Eye a pigmented disc on body margin near antenna. Anterior spiracle with 1 to 5 (median 3) quinquelocular disc pores; posterior spiracle with 0 to 6 (median 2) pores. Lobes absent. Plates absent. Gland spines absent. Gland tubercles absent. Ducts. Dorsal ducts 8-shaped at internal end, minute (2 to 3 μm wide, 10 to 12 μm long); densely distributed in submarginal areas of abdomen and thorax, more thinly scattered on rest of dorsum. Ventral ducts very similar to dorsal ducts, present in a narrow band around submargin of entire body; a few also scattered in submedial areas. Cicatrices absent. Paraphyses absent. Anal opening subcircular to subtriangular, 7 to 10 (median 7.5) μm long, 5 to 10 (median 7.5) μm wide, located near anterior end of abdominal segment VIII; distance from margin 55 to 60 μm (5 to 7 anal lengths) at full maturity, 12 to 50 μm (1.5 to 7 anal lengths) when teneral. Perivulvar pores absent.

Second-instar female exuviae. A single incomplete (ventral surface) specimen is available, permitting the following partial

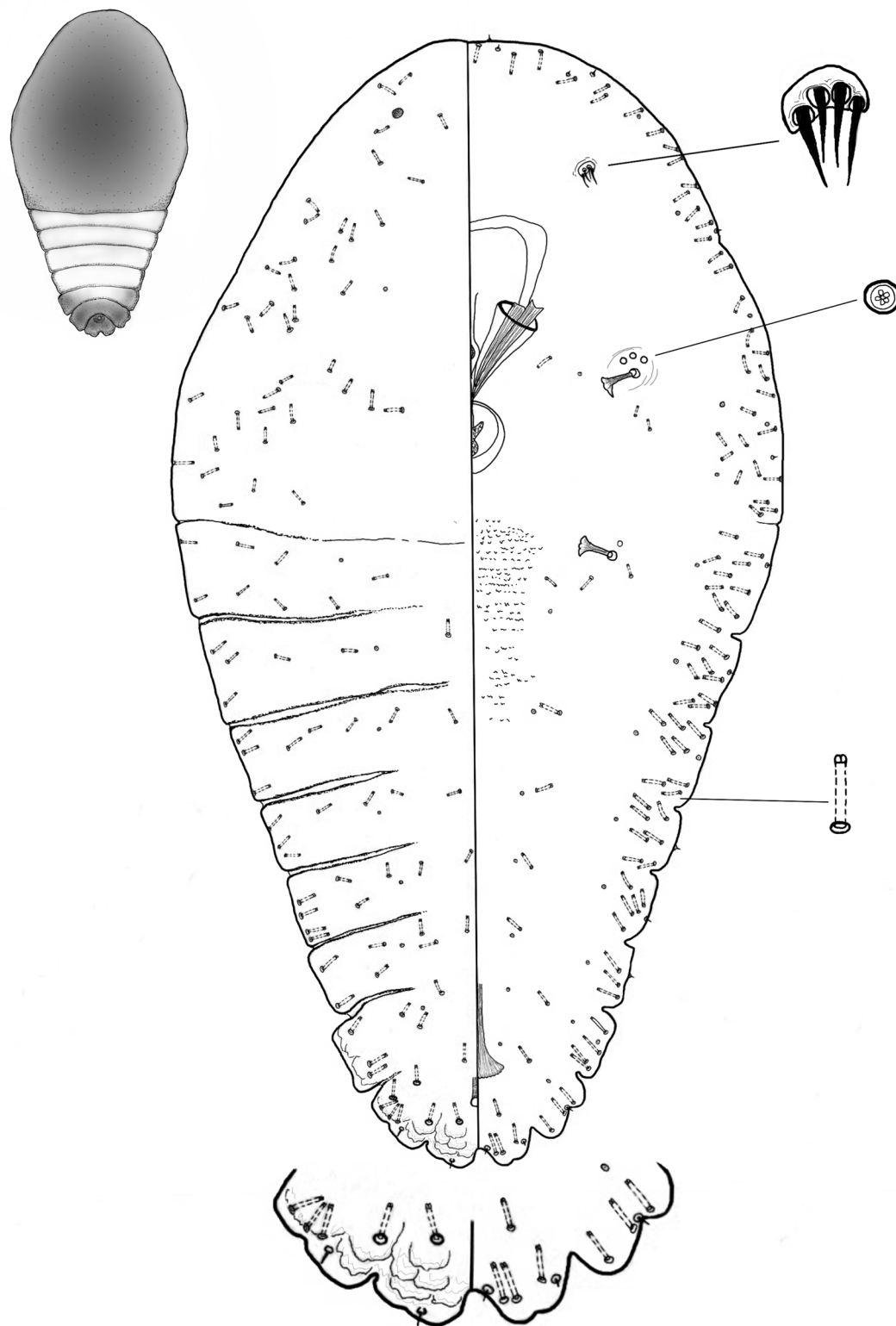


Fig. 11. *Aysenaspis michay* sp. n., slide-mounted adult female.

description, 690 μm long, 400 μm wide. All abdominal segments (I–VIII) free; none fused. Antenna simple, with 4 setae. Distance between antennae 68 μm . Anterior spiracle with 1 quinquelocular disc pore; posterior spiracle without pores. Lobes absent. Plates absent. Gland spines absent. Gland

tubercles absent. Ventral microducts sparsely distributed on submargin of body.

DNA sequences of a fragment of the large ribosomal subunit (28S) of *Aysenaspis michay*, from 2 individuals (PA1500Ad4 and PA1500Aa1) collected at the holotype locality on

31.x.2024, have been deposited in GenBank, accession numbers PV537091-PV537092 (28S).

Etymology. The specific epithet is a Mapuche name for the host. It is an uninflected noun in apposition.

Remarks. Remarkable features of this genus and species are discussed above under the descriptions of Xanthophthalminae and *Aysenaspis*.

Ancepaspidinae Borchsenius

Anotaspis Ferris

Type species. *Anotaspis particula* Ferris. Adult female pupillarial, remaining permanently enclosed within sclerotized cuticle of second instar. Slide-mounted adult female without plates, gland spines, gland tubercles, lobes, or appendages of any kind; dorsal ducts absent; a few exceedingly minute ducts may be present near margin of dorsum; ventral microducts present or absent; antenna with 3 to 4 setae; anterior and posterior spiracles without pores; perivulvar pores, when present, forming a horizontal band on abdominal segment V anterior to vulva; supernumerary perivulvar pores present or absent on abdominal segments IV–II.

Anotaspis paradisi Normark, Normark, and Amouroux, sp. n.

Holotype. Adult female, ex *Retanilla trinervia* (Gillies & Hook.) Hook. & Arn., CHILE, Valparaíso, Parque Nacional La Campana, -32.9435, -71.0856, 6.ii.2019, P. Amouroux, PA960A-0521 (MNHN).

Paratypes. One adult female (remaining within puparium and only partly visible) and 2 puparia, same slide as holotype [fragments (mouthparts) of 2 additional adult females also present on holotype slide] (MNHN); 1 adult female and 1 puparium, same data as holotype, slide PA960A-0520 (USNM); 3 adult females and 3 puparia, ex *Retanilla ephedra* (Vent.) Brongn., CHILE, O'Higgins, Machali, Reserva Nacional Río de los Cipreses, 7.ii.2019, P. Amouroux, PA978A-0085 (MNHN); 3 adult females and 1 second-instar female, ex *Retanilla ephedra*, CHILE, Santiago, “Co El Roble” [Cerro El Roble, -33.0, -71.0], 25.vi.1967, RH Gonzalez 40 to 67 (2 slides, MEUC); 1 adult female, “En hojas de litre” [ex *Lithrea caustica* (Molina) Hook. & Arn.], CHILE, Maipo, El Yeso [-33.67, -70.09], 20.x.1971, “RCh” [Raimundo Charlín] 35-71 (MEUC); 4 adult females, “Tebo” [ex *Retanilla trinervia* (Gillies & Hook.) Hook. & Arn.], CHILE: “Río Clarillo” [most likely Región Metropolitana de Santiago: Río Clarillo, -33.71, -70.52, now Parque Nacional Río Clarillo], xi.1987, [collector not recorded].

Adult female. In life (Fig. 12), on green twig; puparium black, elongate; exuviae marginal, dark brown to black. On microscope slide (Fig. 13), 870 to 890 (median 880) μm long, 440 to 550 (median 480) μm wide; body outline oval, broadest at mesothorax or metathorax; without indentations between any body segments. Cuticle membranous throughout. **Antenna** simple, with 4 setae. Distance between antennae 75 to 100 (median 85) μm . **Eye** inconspicuous or absent. **Perispiracular pores** absent. **Lobes** absent. **Plates** absent. **Gland spines** absent. **Gland tubercles** absent. **Ducts.** Dorsal ducts absent. Ventral

microducts numerous, in submarginal and submedial areas of abdomen and submedial area of metathorax. **Cicatrices** absent. **Paraphyses** absent. **Anal opening** subcircular, about 12 μm in diameter, located about level with vulva, 55 to 65 μm from posterior margin of body. **Perivulvar pores** present in horizontal band anterior to vulva on abdominal segment V, with supernumerary groups of pores on ventral submargin of each of abdominal segments IV–II, with a total of 19 to 25 (median 23) pores on each side of segment V, 3 to 4 (median 4) on IV, 2 to 4 (median 3) on III, and 2 to 5 (median 5) on II.

Puparium. On microscope slide (Fig. 14), 1280 to 1430 (median 1370) μm long, 510 to 620 (median 550) μm wide; outline slightly obovate, broadest at mesothorax; with distinct marginal indentations between body segments from prothorax to posterior end of abdomen, and one additional indentation within each of abdominal segments IV–VI or III–VI. Cuticle very strongly sclerotized (mostly opaque on microscope slide) on cephalothorax and abdominal segment I, less strongly sclerotized (mostly translucent or transparent on microscope slide) on abdominal segments II–VIII. Thus, cephalothoracic features mostly not visible, abdominal features mostly visible. With 2 or 3 pairs of pygidial lobes; L1 bilobulate, each lobule rounded at apex, lobules similar in size and shape but medial lobule positioned more prominently on body margin; L2 bilobulate, similar in size and shape to L1; L3 variable, trilobulate when fully developed, with 2 lobules smaller in size and similar in shape to those of L1 and L2, and a third lobule on anterior marginal prominence of segment VI, roughly rectangular in shape and serrulate along apical margin. With a pair of broad-based gland spines present between L1 and a single broad-based gland spine on margin in posterior portion of each of segments VII–V; segment IV with 3 gland spines, III with 3 to 4, II with 3 to 5, I with 1 to 2; cephalothorax apparently with a sparse row of small gland tubercles near margin. **Ducts.** One dorsal marginal duct present at each indentation of body margin on abdomen: one between L1, one at the posterior boundary of each abdominal segment from VII to II or I, and one nearer the anterior boundary of each of segment from VI to II or I. Ducts 2-barred, with orifices oriented parallel to body margin; orifices of posteriormost ducts broad, becoming much narrower anteriorly; duct between L1 about 15 μm long, orifice about 8 μm wide; a series of submarginal dorsal ducts also present, similar in size to nearby dorsal ducts, with orifices slightly narrower; 1 to 2 on abdominal segment VII, 2 on each of segments VI–III. Anal opening subcircular or oval, 11 to 18 μm long, 12 to 14 μm wide, located 45 to 65 μm from posterior margin of body.

Second-instar female. On microscope slide (Fig. 15), 840 μm long, 520 μm wide; outline oval, broadest at metathorax; cephalothorax without marginal indentations between body segments, abdomen with 1 to 3 indentations per segment. Cuticle membranous throughout. Antenna simple, with 4 setae. Distance between antennae 45 μm . Eye inconspicuous or absent. Perispiracular pores absent. With 3 pairs of pygidial lobes—L1 bilobulate, L2 trilobulate, and L3 bilobulate—each lobe with medial lobule rounded at apex and other lobule or lobules quadrate. Plates absent. With a pair of broad-based gland spines present between L1 and a single broad-based gland spine on margin in posterior portion of each of segments VII–V and



Fig. 12. Habitus of *Anotaspis paradisi* sp. n. Scale covers of adult females, immature females, and immature males on an infested green twig of *Retanilla trinervia*, Parque Nacional La Campana, Valparaíso. Photo by Patrich Cerpa.

2 broad-based gland spines on each of segments IV–I; with a sparse row of duct tubercles on ventral submargin of cephalothorax. Ducts. Dorsal ducts 2-barred, only slightly longer than broad. One dorsal marginal duct present at each indentation of body margin on abdomen, its orifice parallel with body margin; 2 to 3 submarginal ducts, slightly smaller than marginal ducts, present on each body segment from abdominal segment VII to metathorax; 1 to 3 submedial ducts, smaller than submarginal ducts, present on each of abdominal segments V–III. Cicatrices absent. Paraphyses absent. Anal opening circular, 12 µm in diameter, located 48 µm from posterior margin of body.

DNA sequences of a fragment of the large ribosomal subunit (28S) and cytochrome oxydase I of members of the type series of *Anotaspis paradisi* have been deposited in GenBank, accession numbers PQ219558–PQ219559 (COI), PQ211154–PQ211155 (28S).

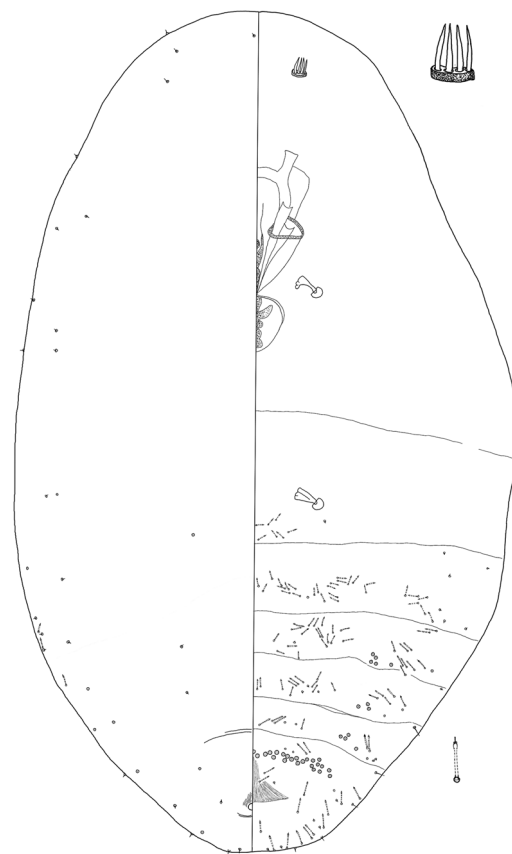


Fig. 13. *Anotaspis paradisi* sp. n., slide-mounted adult female.

Remarks. When describing the genus *Anotaspis*, Ferris (1941, SIII-269) wrote “The chief feature of the genus is its featurelessness!” The adult female of *Anotaspis paradisi* resembles that of the type species, *Anotaspis particula*, in being pupillarial, with multisetose antennae and a simple oval shape, without any gland spines, plates, lobes, or other appendages, and without pores by the anterior or posterior spiracles. The adult female of *A. paradisi* differs from *A. particula* in having perivulvar pores and ventral microducts (absent in *A. particula*). The puparium of *A. paradisi* resembles that of *A. particula* in being heavily sclerotized and obovate, with marginal indentations between most body segments. It differs from that of *A. particula* in having pygidial lobes, dorsal ducts, and gland spines (absent in *A. particula*).

Etymology. The specific epithet is the genitive form of Latin *paradisum*, meaning park, orchard, Eden. It refers to the type locality in Valparaíso, originally meaning valley (*valle*) of paradise (*paraíso*).

Key to Subfamilies of Diaspididae, Modified from Normark et al. (2019)

Abbreviations: AF = adult female; AM = adult male; 2F = second-instar female; 2M = second-instar male; CR = crawler (first-instar nymph); M = male (any stage). L1 = first pair of pygidial lobes (trullae), occurring on abdominal segment VIII;



Fig. 14. *Anotaspis paradisi* sp. n., slide-mounted puparium (sclerotized cuticle of second-instar female).

L2=second pair of pygidial lobes, occurring on segment VII; L3=third pair of pygidial lobes, occurring on segment VI. When a range of values is given, followed by one or more values in parentheses, eg 0 to 3 (0), the figure in parentheses gives the modal or most commonly occurring value or values, unless otherwise noted.

1. AF completely or partially enclosed within cuticle of 2F, not secreting an extensive scale cover; without plates or gland spines; ducts absent or minute; perivulvar pores, when present, forming a horizontal band anterior to vulva; antenna multisetose (rarely unisetose); pygidium comprising only abdominal segments VI–VIII or VII–VIII; with 0 to 7 pairs of sclerotized or hyaline marginal lobes on abdomen; median lobes, if present, usually with serrate apical margin, often with 2 or more lobules; other lobes if present each with 1 to 6 lobules; 2F body margin without plates; with or without gland spines; with or without ducts—when marginal ducts present, these are 2-barred and often short and wide (barrel-shaped); CR abdominal segments III–VI each with 2 submedian setae (1 dorsal, 1 ventral); head without dorsal ducts; abdominal segment II with a submedian dorsal duct; M diploid,

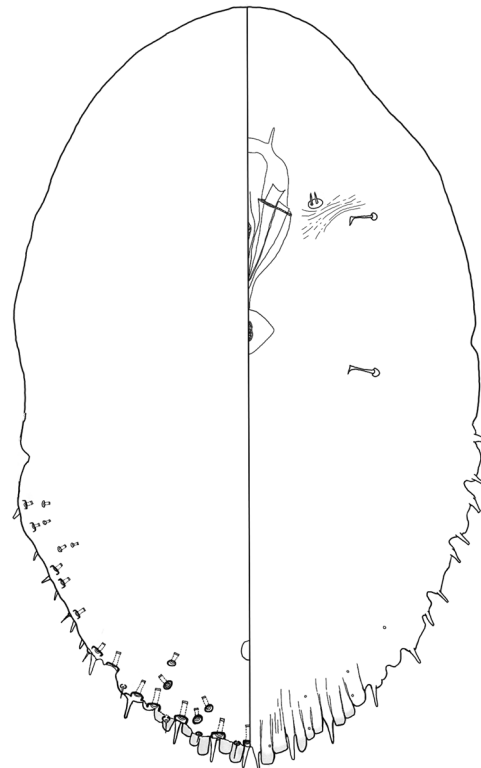


Fig. 15. *Anotaspis paradisi* sp. n., slide-mounted second-instar female.

with half of the chromosomes heterochromatic; antenna 6-segmented, without annulations; Nearctic and Neotropical ... 2

- AF secreting a scale cover often much larger than exuviae of 2F, or remaining enclosed within cuticle of 2F; usually with gland spines, or plates, or both; ducts usually present, often large; perivulvar pores, when present, usually in 4 to 5 groups, some pores situated posterolaterad of vulva; antenna unisetose or (less commonly) multisetose; pygidium usually comprising abdominal segments V–VIII; with 0 to 5 (usually 1 to 3) pairs of sclerotized marginal lobes on abdomen; median lobes various, but if present always unilobulate; other lobes if present each with 1 to 2 (rarely 3) lobules; 2F body margin with or without plates; with or without gland spines; usually with ducts, which may be 1- or 2-barred and of various sizes and shapes; CR abdominal segments III–VI each with 1 submedian seta, which may be dorsal or ventral; head with or without dorsal ducts; if submarginal dorsal ducts are absent from head, abdominal segment II lacks a submedian dorsal duct; M haploid, without heterochromatic chromosomes or (less commonly) diploid, with half of the chromosomes heterochromatic; antenna 5- or 6-segmented, with or without annulations; widespread ... 3
2. AF partially enclosed within dehiscent exuviae of 2F (not pupillarial); segment VI free, not fused to posterior segments; with 0 to 7 pairs of sclerotized or hyaline marginal lobes on abdomen; lobes, when present, each with 2 to 6 lobules... **XANTHOPHTHALMINAE**
 - AF completely enclosed within intact sclerotized cuticle of 2F (pupillarial); segment VI fused to

posterior segments, forming pygidium; with 0 to 3 (usually 0) pairs of sclerotized marginal lobes on abdomen; lobes, when present, each with 1 to 2 lobules... **ANCEPASPIDINAE**

3. **AF** antenna with 3 to 8 setae; plates distinctive, consisting of a dorsoventrally thickened portion that appears bifurcate or trifurcate and a thinner marginal portion stretched between the tines; without fringing on plates and without gland spines; without pores near posterior spiracle; first 3 pygidial lobes similar in shape, unilobular; without notches; dorsal ducts very thin, resembling ventral microducts; **M** diploid, with half of the chromosomes heterochromatic; circumtropical, extending to temperate regions of South Africa and Australia, and in greenhouses ... **FURCASPIDINAE**

- **AF** antenna unisetose or (less commonly) multisetose; plates, when present, of uniform thickness and often fringed; with or without gland spines; with or without pores near posterior spiracle; lobes various; ducts various, dorsal ducts often wider than ventral microducts; **M** haploid, without heterochromatic chromosomes or (less commonly) diploid, with half of the chromosomes heterochromatic; widespread ... 4

4. **AF** usually with fringed plates and without gland spines; **L2** and **L3**, when present, unilobular; ducts 1- or 2-barred; orifices of marginal macroducts, if oblong, with long axis usually parallel to body margin; pores by anterior spiracle present or absent, when present usually 5-locular; **2F** usually with fringed plates; **L2** unilobular; **CR** abdominal segment II with submedian dorsal duct; abdominal segments III–VI without dorsal submedian setae; abdominal segments IV–VI each without ventral submedian seta; head and mesothorax each with submarginal or submedial dorsal duct; terminal segment of antenna with 2 apical setae; tarsus with seta near base of claw; tarsus and tibia fused or separated by a septum; **AM** midcranial ridge with dorsal branches reduced; tubercular ocelli present; pronotal ridges present; abdomen without dorsal setae on segments IV–VII; **M** haploid without heterochromatic chromosomes or diploid with half of the chromosomes heterochromatic ... **ASPIDIOTINAE**

- **AF** usually without fringed plates and with gland spines; **L2** usually bilobular, **L3** bilobular or unilobular; ducts usually 2-barred; orifices of marginal macroducts, if oblong, with long axis oblique or perpendicular to body margin; pores by anterior spiracle usually present, usually 3-locular; **2F** usually without fringed plates; **L2** usually bilobular; **CR** abdominal segment II without submedian dorsal duct; abdominal segments III–VI each with dorsal submedian seta; abdominal segments IV–VI each with ventral submedian seta; head and mesothorax without submarginal or submedial dorsal ducts; terminal segment of antenna with 1 apical seta; tarsus with or without seta near base of claw; tarsus and tibia separated by a septum; **AM** midcranial ridge with dorsal branches present; tubercular ocelli absent; pronotal ridges absent; abdomen with dorsal setae on segments IV–VII; **M** haploid, without heterochromatic chromosomes ... **DIASPIDINAE**

Global Key to Adult Females of Xanthophthalminae

1. Sclerotized or hyaline marginal lobes present on abdomen, each with 2 to 6 lobules; gland tubercles present on submargin of cephalothorax; ducts 2-barred; Chile (*Austraspis*, gen. n.) 2
 - Abdomen without lobes; gland tubercles absent; ducts 8-shaped at internal end; Mexico and Cuba to Chile 5
2. Lobules on pygidium sclerotized, subtended by basal sclerosis longer than lobule, separated from each other by a narrow space; with fewer than 20 gland tubercles on each side of cephalothorax; cephalothorax becoming sclerotized at full maturity; on *Araucaria araucana* *Austraspis pehuen*, sp. n.
 - Lobules on pygidium hyaline, without basal sclerosis, adjacent lobules often appressed or partially fused; with more than 30 gland tubercles on each side of cephalothorax; cephalothorax remaining membranous; on *Drimys winteri* 3
3. With a submarginal row of more than 65 gland tubercles on each side of body; with more than 10 pores by posterior spiracle; with more than 12 pores by anterior spiracle; with more than 17 lobules on each side of abdomen; northern Chile (Coquimbo) *Austraspis relicta*, sp. n.
 - With a submarginal row of fewer than 55 gland tubercles on each side of body; usually with fewer than 10 pores by posterior spiracle; usually with fewer than 12 pores by anterior spiracle; usually with fewer than 17 lobules on each side of abdomen; southern Chile (Los Lagos to Magallanes) 4
4. With 2 to 5 pores by posterior spiracle and 5 to 6 by anterior spiracle; with fewer than 11 lobules on each side of abdomen; Los Lagos *Austraspis llanquihue*, sp. n.
 - With 3 to 11 (median 6) pores by posterior spiracle and 5 to 17 (median 9) by anterior spiracle; usually with more than 11 lobules on each side of abdomen; Aysén and Magallanes *Austraspis foye*, sp. n.
5. Antenna with a single seta; without pores near anterior spiracles; on *Arecaceae*, Mexico and Cuba to Panama and Trinidad *Xanthophthalma concinnum* Cockerell & Parrott in Cockerell, 1899
 - Antenna with 4 setae; with quinquelocular pores near anterior spiracle; on *Berberis*, Chile *Aysenaspis michay*, sp. n.

Global Key to Adult Females of Ancepaspidinae

1. Margin of pygidium entire, without lobes, incisions, projections, or divisions 2
 - Margin of pygidium with sclerotized or hyaline lobes, or deeply incised to form broad divisions or projections 5
2. With perivulvar pores 3
 - Without perivulvar pores 4

3. Anterior spiracle with associated pores; abdominal segments II–IV without pores; on *Ulmus*, southeastern USA *Fissuraspis ulmi* (Hoke)
 - Anterior spiracle without pores; abdominal segments II–IV with supernumerary perivulvar pores; on *Retanilla*, central Chile *Anotaspis paradisi*, sp. n.
4. With a sclerotized band on dorsum of pygidium outlining a roughly circular area immediately posterior to anus; Arizona *Anceaspis edentata* (Ferris)
 - Without sclerotized band on dorsum of pygidium; Panama *Anotaspis particula* Ferris
5. Margin of pygidium incised or exerted to form 3 or more broad projections; otherwise without sclerotized, hyaline, or membranous lobes; USA and Mexico 6
 - Margin of pygidium not incised or exerted, not forming broad projections; with 1 to 3 pairs of sclerotized, hyaline, or membranous lobes; USA to Brazil 9
6. Margin of pygidium incised or exerted to form 3 broad processes; Arizona and Texas to Baja California Sur and Guerrero 7
 - Margin of pygidium incised to form 4 or 9 broad processes; Baja California Sur and Guerrero 8
7. Body outline obovate; pygidium nearly parallel-sided, projecting, deeply incised to form 3 broad, parallel or convergent processes; on *Neltuma*, Arizona and Texas to Baja California Sur *Anceaspis tridentata* (Ferris)
 - Body outline turbinate; pygidium bluntly rounded, not projecting, with portions of pygidial margin exerted to form 3 broad, divergent processes; Guerrero *Nicholiella digitata* Ferris
8. Margin of pygidium incised to form 4 broad processes; on *Quercus*, Guerrero *Anceaspis quadridentata* Ferris
 - Margin of pygidium incised to form 9 broad processes; on *Lysiloma*, Baja California Sur *Anceaspis novemdentata* Ferris
9. Perivulvar pores present in a broad arc anterior to vulva; pores present or absent near anterior spiracle; USA to Panama (*Pelliculaspis* Ferris) 10
 - Perivulvar pores absent; pores present near anterior spiracle; USA to Brazil 12
10. With 3 pairs of pygidial lobes; L1 bilobular; gland tubercles present on dorsal submargin of thorax; Panama *Pelliculaspis pellita* Ferris
 - With 2 pairs of pygidial lobes; L1 unilobular; gland tubercles absent; Texas and Panama 11
11. L2 a simple, unilobulate point; one or more pores present near anterior spiracle; Texas *Pelliculaspis celtis* McDaniel
 - L2 bilobulate, apically toothed; without pores near anterior spiracle; Panama *Pelliculaspis dura-pyga* Ferris
12. With 2 pairs of lobes; L1 and L2 both slight, membranous, rounded; on Myrtaceae, Brazil *Costalimaspis eugeniae* Lepage
 - With 1 pair of lobes; L1 robust, sclerotized, subrectangular; on *Sideroxylon*, Arizona *Nicoliella bumeliae* Ferris

Discussion

Molecular and morphological evidence both support the hypothesis that the new species *Anotaspis paradisi* belongs to the subfamily Ancepaspidinae and that the new genera *Austraspis* and *Aysenaspis* form a clade that falls outside all 4 of the subfamilies of Diaspididae recognized by Normark et al. (2019). Based on morphology, we have assigned *Austraspis* and *Aysenaspis* to the revived subfamily Xanthophthalminae. Under this system, Chile becomes the center of distribution for the subfamily Xanthophthalminae, with 5 of the 6 known species, and the Americas become the center of endemism for diaspidid subfamilies; of the 5 subfamilies of Diaspididae, 2 are endemic to the Americas (Ancepaspidinae and Xanthophthalminae), while the other 3 occur nearly worldwide (Furcaspidinae, Aspidiotinae, and Diaspidinae).

The phylogenetic position of Xanthophthalminae is not resolved by our analysis, but the available evidence suggests that it is likely to break one of the more basal internodes in the tree of Diaspididae, and thus to provide information about the character states of the most recent common ancestor of the family. This potential is all the greater because *Austraspis* species are unlike other species of Xanthophthalminae and unlike Ancepaspidinae in that they have a rich system of ducts and marginal appendages.

Most of the cuticular structures on which diaspidid taxonomy has been largely based—lobes, pores, plates, gland spines, ducts, and so on—are involved in the secretion of the scale cover. Such structures are usually lost in pupillarial species, at least in the adult female, which thus tend to converge on a set of similar, rather simplified, blob-like morphologies (the “featurelessness” noted by Ferris in his description of *Anoplaspis* and exemplified anew by *A. paradisi*, Fig. 13). *Austraspis* represents a rare glimpse of an unsimplified member of a lineage that diverged from other diaspidid lineages early in the history of the family. Of course, just because a lineage is phylogenetically isolated and species-poor does not in itself imply that it is in any way basal or primitive (Krell and Cranston 2004), but in the case of *Austraspis*, the host plants too are phylogenetically isolated and species poor, and—crucially—have excellent fossil records indicating little morphological change since the Cretaceous (Poole and Francis 2000, Escapa and Catalano 2013). It is plausible to conjecture that the relationships of *Austraspis* species with their hosts are ancient ones, and that in the relatively cool, stable, isolated habitats of the austral temperate rainforests and *Araucaria* woodlands, *Austraspis*, too, like its hosts, may have undergone relatively little morphological change, at least compared to other armored scale insects.

In this context, it is intriguing that the marginal and submarginal appendages of *Austraspis* species are imperfectly differentiated into distinct types. We have called the most prominent marginal pygidial appendages “lobules”; like the lobules of other Diaspididae, they are at least apically sclerotized or hyaline, and some have paraphysis-like basal scleroses. But the lobules of some *Austraspis* species differ from those of other Diaspididae in being partially membranous; they are also unusual in being variable both within and between segments. They most resemble the lobules of other Diaspididae in more posterior segments and in more posterior positions within segments. Often the anteriormost lobule of a segment appears to

be entirely membranous, resembling a plate—a pectina, in Takagi's (2002) terminology. Lobules also have a tendency to become more plate-like on more anterior pre-pygidial abdominal segments, becoming less opaque and sclerotized, more hyaline, and ultimately membranous (in *A. pehuen*) or less stiffly hyaline and more membranous (in the *Drimys*-feeding species). In *A. relict*a in particular, some lobules resemble duct tubercles in having a single microduct opening near the apex of the membranous portion, and indeed in this species the row of lobules on the margins of segments V–VIII is nearly contiguous with the row of duct tubercles on the submargins of the anterior segments, with the structures on abdominal segments III and IV appearing to be intermediate between the 2 types of appendage; like gland tubercles they are membranous; like lobules, they are directly on the body margin and some appear to be slightly serrate (the serration being due to an irregular apical fringe of membranous tines). The true gland tubercles of abdominal segment II and anterior segments are each subtended by a single duct, opening at the apex of the tubercle. The intermediate structures on segments III and IV have ducts present or absent, and when a duct is present, its opening is not always at the apex of the structure.

Differentiation of serially homologous elements is a pervasive theme in evolution in general and arthropod evolution in particular. In the case of Diaspididae, Takagi has written extensively about the differentiation of the marginal appendages (Takagi 1981, 1990, 2002), but his views can be difficult to interpret and apply, in part because he has explicitly rejected phylogeny as a useful concept and has supposed that hybridization and horizontal gene transfer are rampant (Takagi 2002). A more recent phylogenetic study did not explicitly address the differentiation of the marginal appendages (Normark et al. 2019); its results implied only that the common ancestor of Diaspididae was pupillarial, with few marginal appendages, and that the subsequent morphological diversity of marginal appendages arose rapidly. The present study leaves the relationships between the subfamilies of Diaspididae unresolved. Whatever the precise topology, the most recent common ancestor of the scale-secreting lineages of Diaspididae likely had a relatively undifferentiated system of marginal appendages, perhaps resembling the relatively undifferentiated system of marginal appendages seen in *Austraspis* today.

Specimen Collection Statement

Nagoya Protocol: The authors attest that all legal and regulatory requirements, including export and import collection permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study. For sampling in Chile, we thank the Corporación Nacional Forestal (CONAF) for authorization n°024/2018 and n°008/2024 to collect in protected areas (SNASPE).

Nomenclature

This paper and the nomenclatural acts it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is:

- urn:lsid:zoobank.org:pub:666D0E42-40DD-40CD-8170-55605886630A for the publication
- urn:lsid:zoobank.org:act:C8C01741-C2D4-4867-BC76-2F8FBAF80F0B for *Austraspis* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:EF0D0EB7-84F4-4458-80BC-B353839CC0DF for *Aysenaspis* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:CE451F43-C4AE-4EAD-9F5F-7CFCF10676A4 for *Anotaspis paradisi* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:6108AFC3-A1B5-4282-8F59-262B23958BB0 for *Austraspis foye* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:7852EF60-D2E6-49B3-B369-1DC5640163D4 for *Aysenaspis michay* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:874D2EA8-010E-4BDD-AD3D-5B239D7337DF for *Austraspis relict*a Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:648C367C-FB35-406F-9197-AC7EFFF0F9C8 for *Austraspis pehuen* Normark, Normark & Amouroux
- urn:lsid:zoobank.org:act:FB890561-1AD8-4F56-BC1C-380CCBF089DD for *Austraspis llanquihue* Normark, Normark & Amouroux

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Author Contributions

Benjamin Bo Normark (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Methodology [equal], Resources [equal], Validation [equal], Writing—original draft [lead], Writing—review & editing [lead]), Roxanna Normark (Data curation [supporting], Formal analysis [supporting], Methodology [supporting], Visualization [lead]), Alyson Cabral (Formal analysis [supporting], Investigation [supporting], Visualization [supporting], Writing—review & editing [supporting]), and Paul Amouroux (Conceptualization [equal], Data curation [equal], Formal analysis [supporting], Funding acquisition [lead], Investigation [equal], Project administration [lead], Writing—review & editing [equal])

Supplementary Material

Supplementary material is available at *Insect Systematics and Diversity* online.

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Conflicts of Interest

No conflicts of interest.

Data Availability

Collection data for samples collected by PA are available at Global Biodiversity Information Facility as dataset “Diaspididae de Chile” (<https://doi.org/10.15468/sbt4d3>)

Raw files from the phylogenetic workflow are available in Dryad as dataset “28S Diversity of Diaspididae subfamilies for phylogenetic analysis” (<https://doi.org/10.5061/dryad.wstqjq304>)

DNA sequences were deposited in NCBI GenBank® under the accession number PQ219562 (COI) for *Austraspis foye*; PQ219560 (COI) and PQ211156–PQ211157 (28S) for *Austraspis llanquihue*; PQ219561 (COI) and PQ211153 (28S) for *Austraspis pehuen*; PQ219558–PQ219559 (COI) and PQ211154–PQ211155 (28S) for *Anotaspis paradisi*; and PV537091–PV537092 (28S) for *Aysenaspis michay*.

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